

LAMPOCTEIS CRUENTIVENTER GEN. NOV., SP. NOV.: A NEW
MESOPELAGIC LOBATE CTENOPHORE, REPRESENTING THE
TYPE OF A NEW FAMILY (CLASS TENTACULATA, ORDER
LOBATA, FAMILY LAMPOCTENIDAE, FAM. NOV.)

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ABSTRACT

This paper describes a new genus and species of mesopelagic ctenophore in the Order Lobata, *Lamprocteis cruentiventer*, which was first collected in 1979 off southern California and later collected and studied in detail from 1991 to 1999 in Monterey Bay. This ctenophore differs from all previously described lobate ctenophores in two major ways: (1) all of the meridional canals have blind aboral endings, and (2) the body is penetrated by a deep notch located between the adjacent subtentacular comb rows at the level of the infundibulum. Because of these distinctive features, we feel justified in erecting a new family, the Lampoctenidae, for this species. Several other features (the large pigmented stomodaeum, the large diverticulate paragastric canals and the well-developed, strongly iridescent comb plates) distinguish this species. Based on the discovery of *L. cruentiventer*, we have tentatively revised the diagnoses of the families Bolinopsidae and Eurhamphaeidae to take into account the spatial relationships of the adradial and meridional canals. We provisionally recognize the following families in the Order Lobata as valid: Bathocyroidae, Bolinopsidae, Eurhamphaeidae, Lampoctenidae, Leucotheidae, and Ocyropsidae.

The Ctenophora is a small, homogeneous phylum of exclusively marine invertebrates, with uncertain affinities with other metazoan groups (Krumbach, 1925; Harbison, 1985; Lipscomb et al., 1998). All extant ctenophores have eight meridional bands of fused cilia, called comb rows, at some stage of their development, and all of the known species are predators. The present classification of the Ctenophora is not phylogenetic: at least one order, the Cydippida is clearly polyphyletic, while the other three large orders, the Beroida, Lobata and Cestida are most likely monophyletic (Harbison, 1985).

The evidence for monophyly in the Lobata is extremely strong, since it is based on two major synapomorphic structures, the auricles and the oral lobes. Both structures are used in feeding, body orientation and locomotion, and vary considerably between genera. The auricles may be long and sinuous (as in species of *Leucothea* Mertens, 1833), or short and rigid (as in species of *Ocyropsis* Mayer, 1912), while the oral lobes may be voluminous (as in species of *Leucothea*) or compact (as in *Eurhamphaea vexilligera* Gegenbaur, 1856). Both structures are used for feeding in concert with the tentacular apparatus, which is embedded in the margins of the mouth in all known lobate ctenophores, except in species of *Ocyropsis*, in which the tentacular apparatus is either reduced in *O. maculata* (Rang, 1827) or absent in *O. crystallina* (Rang, 1827).

Although the Lobata form a homogeneous group, relationships within the order are not clear at present. However, the various genera within the order may be provisionally divided into two major groups, based on the ways in which the adradial canals connect with the meridional canals. In one group, all adradial canals connect with the meridional canals at the aboral ends of the latter (this includes species in the genera *Bathocyroe* Madin and Harbison, 1978, *Bolinopsis* Mayer, 1912, *Mnemiopsis* Agassiz, 1860, and *Ocyropsis*). In the second group, the substomodaeal adradial canals connect with the meridional ca-

nals at their aboral ends, but the subtentacular adradial canals connect with the meridional canals at some point oral to their ends (usually approximately at the level of the infundibulum). Therefore, the aboral endings of the subtentacular meridional canals are blind in this group (which includes species in the genera *Deiopea* Chun, 1879, *Eurhamphaea*, *Kiyohimea* Komai and Tokioka, 1940, and *Leucothea*). In this paper, we report on a new lobate ctenophore in which all of the meridional canals have blind aboral endings. Since this feature has not previously been reported for any lobate ctenophore, we feel justified in placing this new species in a new genus, *Lampocteis*, and in a new family, Lampoctenidae.

MATERIALS AND METHODS

The holotype was collected in 1979 from DSRV ALVIN with a slurp gun similar to the one used by Madin and Harbison (1978). Because the slurp gun was located in a position where the observers could not see it, and six specimens (two of which were ctenophores) were collected and mixed together in the single canister, the depth at which the holotype was collected was not recorded. One observer (J. Purcell) noted a red lobate ctenophore with brilliantly sparkling comb rows at 775 m, which could have been the holotype, or another specimen of *Lampocteis cruentiventer*. After collection, N. R. Swanberg photographed the specimen in a chilled photo tank on board the RV LULU. Ellen Chase drew Plate 1 from these photos in consultation with the senior author. The holotype disintegrated immediately when preserved in 5% buffered formalin.

From 1991 to 1999, additional specimens were collected and in situ observations were made by scientists at the Monterey Bay Aquarium Research Institute (MBARI) with the remotely operated vehicle (ROV) VENTANA (Robison, 1993). The principal tool for in situ observations was a high-resolution color video camera (Sony DXC 3000) fitted with a surface-controlled, 5.5 to 40 mm zoom lens that provided telephoto, wide angle, and macro-imaging capabilities. The video signal was conveyed to the surface support vessel (RV POINT LOBOS) through optical fibers at the core of the ROV's tether. At the surface, the video signal was viewed on a monitor and recorded on BetaCam tape. After each dive, this information was transcribed into a database and cross-referenced with synoptic data on depth, temperature, salinity, and oxygen concentration. Because of the maneuverability of the ROV, it was possible to view and record undisturbed in situ specimens of this ctenophore from virtually all angles, thus facilitating this description.

Specimens were collected by the ROV in 7.5-L static samplers (Youngbluth, 1984). Captured specimens were transported to the laboratory ashore, where they were examined, photographed, and subsequently preserved in 4% buffered glutaraldehyde. Preservation of intact specimens is very difficult for this species, such that all MBARI specimens that were larger than 2 cm in overall length disintegrated in the preservative.

Some specimens were frozen at -80°C for molecular analysis. Genomic DNA was extracted from frozen tissue using a modified CTAB-DTAB protocol (Gustinich et al., 1991). The large and small subunit rRNA genes were amplified using slightly modified universal primers developed by Scholin and Anderson (1994). Thus far, a portion of the small subunit rRNA gene has been sequenced (GenBank AF268381), and the remaining portion of the small subunit rRNA and the large subunit rRNA genes are currently being sequenced by the second author.

RESULTS

Order Lobata

Family **Lampoctenidae** new family

Diagnosis.—Lobate ctenophores in which all meridional canals end blindly aborally. The family contains a single genus.

Type Genus.—*Lampocteis* gen. nov.

Etymology.—Formed from the stem of *Lampocteis*, “Lampocten-“

Lampocteis new genus

Diagnosis.—Lobate ctenophores in which all meridional canals end blindly aborally. Deep notch present at level of infundibulum between adjacent subtentacular comb rows. Stomodaeum large, strongly pigmented, capable of expansion in the tentacular plane. Paragastric canals large, with diverticula. The genus is monotypic.

Type Species.—*Lampocteis cruentiventer* sp. nov.

Etymology.—Compound masculine noun derived from the Greek λαμπός, “bright, shining, brilliant”, and Greek κτεῖς, κτενός, “comb”. The generic name refers to the exceptionally bright iridescence of the comb rows caused by diffraction of light through the broad comb plates.

Lampocteis cruentiventer new species

Type Material.—Holotype collected on DSRV ALVIN dive 968 (9 September 1979) pilot, G. Ellis, observers, V. L. McAlister and J. E. Purcell. Location of dive: 32°32'N, 117°54'W, off San Diego, California. Depth of bottom 1227 m. Time of collection between 1617 and 1845 PDST. Depth of collection between 1130 and 640 m. A preserved specimen (collected 24 July 1991 at a depth of 679 m in the Monterey Submarine Canyon (36°42'N, 122°02'W) and copies of the photographs of the holotype have been deposited in the collections of the California Academy of Sciences (CASIZ #110779). The deposited specimen was considerably distorted and shriveled by the fixative. While the eight comb rows remained intact, the oral lobes dissolved, and the internal structure could no longer be discerned. The preserved specimen thus bears little resemblance to its appearance in life. Additional specimens are stored at MBARI, and images of *L. cruentiventer* have been posted on the World Wide Web (<http://www.mbari.org/rd/midwater/Lampocteis/>).

Etymology.—New masculine noun in apposition formed from Latin *cruentus*, “blood-red”, and Latin *venter*, “belly”. Refers to the exceptionally brilliant red stomodaeum of this species.

Examination of Material.—The holotype (Figs. 1,2) was sketched and photographed. It could not be preserved intact, so our description is based on the photographs, drawings, and notes made at the time. The description of the holotype is supplemented by images and additional collections made by MBARI in the Monterey Submarine Canyon (Fig. 3). Unless specifically noted, all sentences in the following diagnosis and description refer to the holotype.

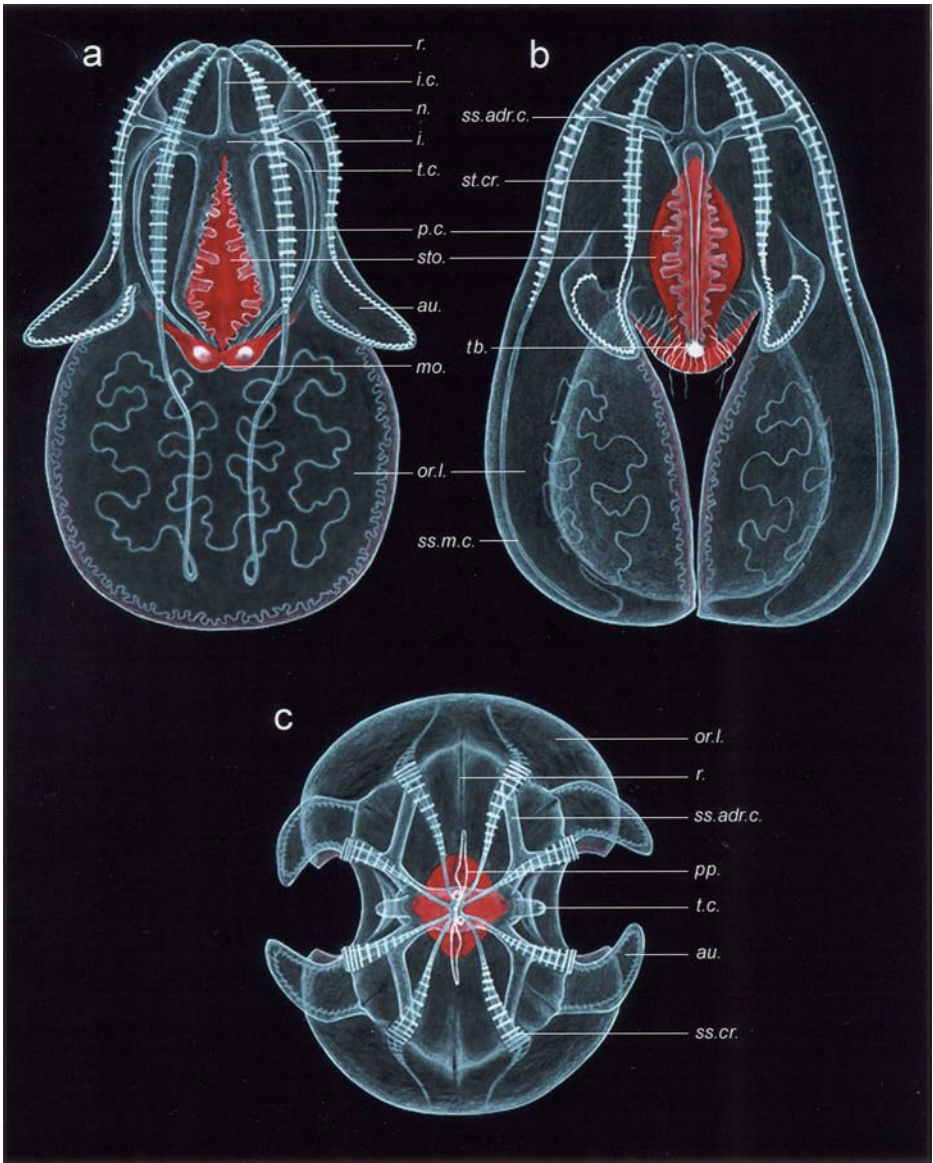


Figure 1. Drawing of the holotype of *Lampocteis cruentiventer* in the (a) tentacular plane, (b) stomodaeal plane, and (c) aboral view. Abbreviations: *au.*, auricle; *i.*, infundibulum; *i.c.*, infundibular canal; *mo.*, mouth; *n.*, notch; *or.l.*, oral lobe; *p.c.*, paragastric canal; *pp.*, pole plate; *r.*, ridge; *ss.adr.c.*, substomodaeal adradial canal; *ss.cr.*, subtentacular comb row; *ss.m.c.*, substomodaeal meridional canal; *st.cr.*, subtentacular comb row; *sto.*, stomodaeum; *tb.*, tentacle bulb; *t.c.*, tentacular canal.

Diagnosis.—Lobate ctenophore with red stomodaeum, expanded in stomodaeal plane and capable of wide expansion in tentacular plane. Body deeply excavated between adjacent subtentacular comb rows at level of infundibulum. Paragastric canals massive, with blindly ending diverticula, which are branched in some MBARI specimens. Tentacular canals arising at infundibulum at junctions of interrarial canals. Interrarial canals short, branching to form adradial canals. All adradial canals connect with meridional canals at

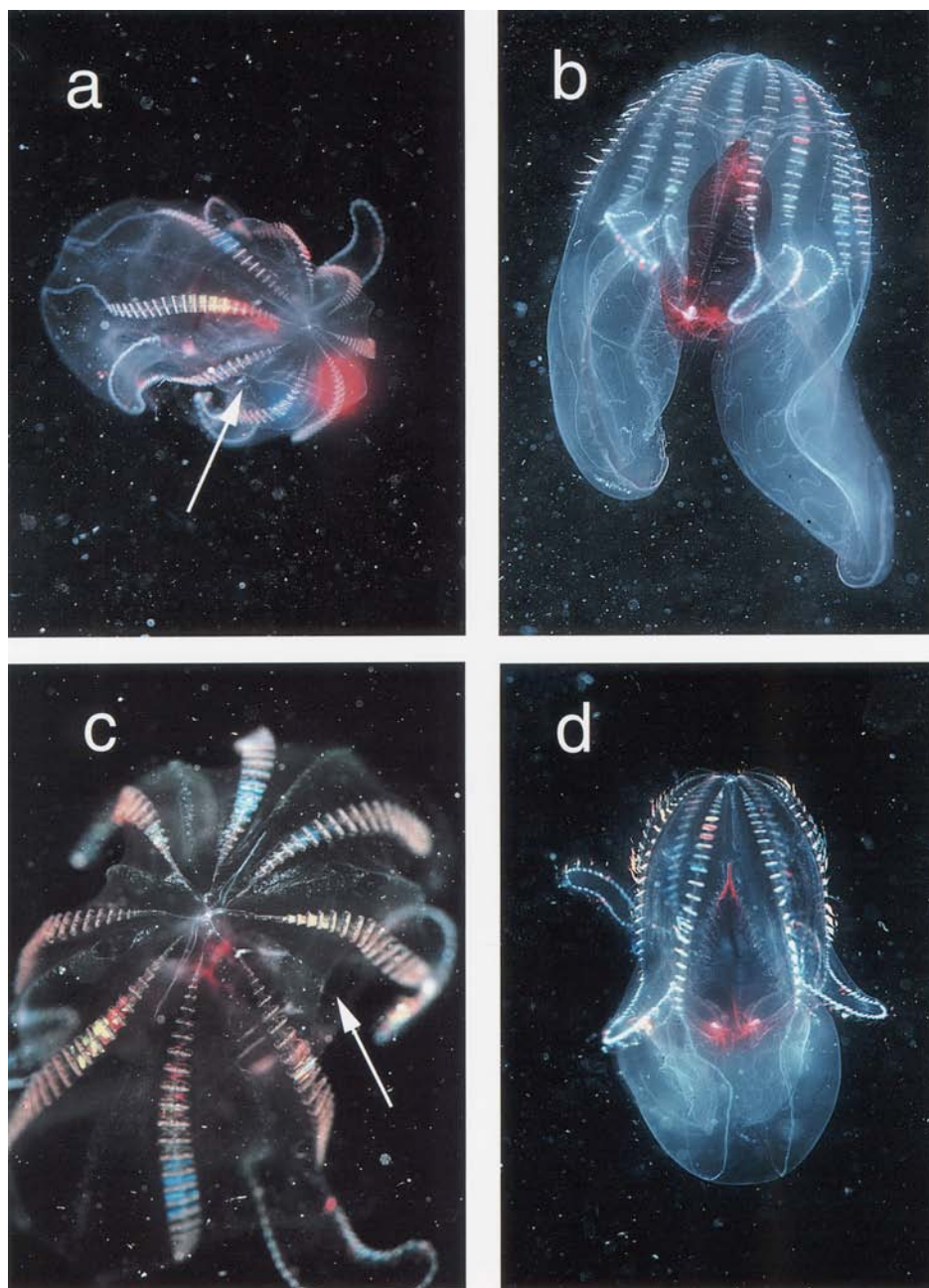


Figure 2. Laboratory photographs of the holotype of *Lampocteis cruentiventer*. Overall body length 5 cm. The position of the notch is indicated with an arrow. (a) Aboral view showing the notch, pole plates, and body ridges. (b) View in the stomodaeal plane, showing the flask-shaped stomodaeum surmounted by the large, diverticulate paragastric canal. (c) Aboral view—close-up showing the ridges and pole plates. The opening of the notch can be seen between the subtentacular comb rows. (d) View in the tentacular plane showing both tentacle bulbs and the diamond-shaped stomodaeum.

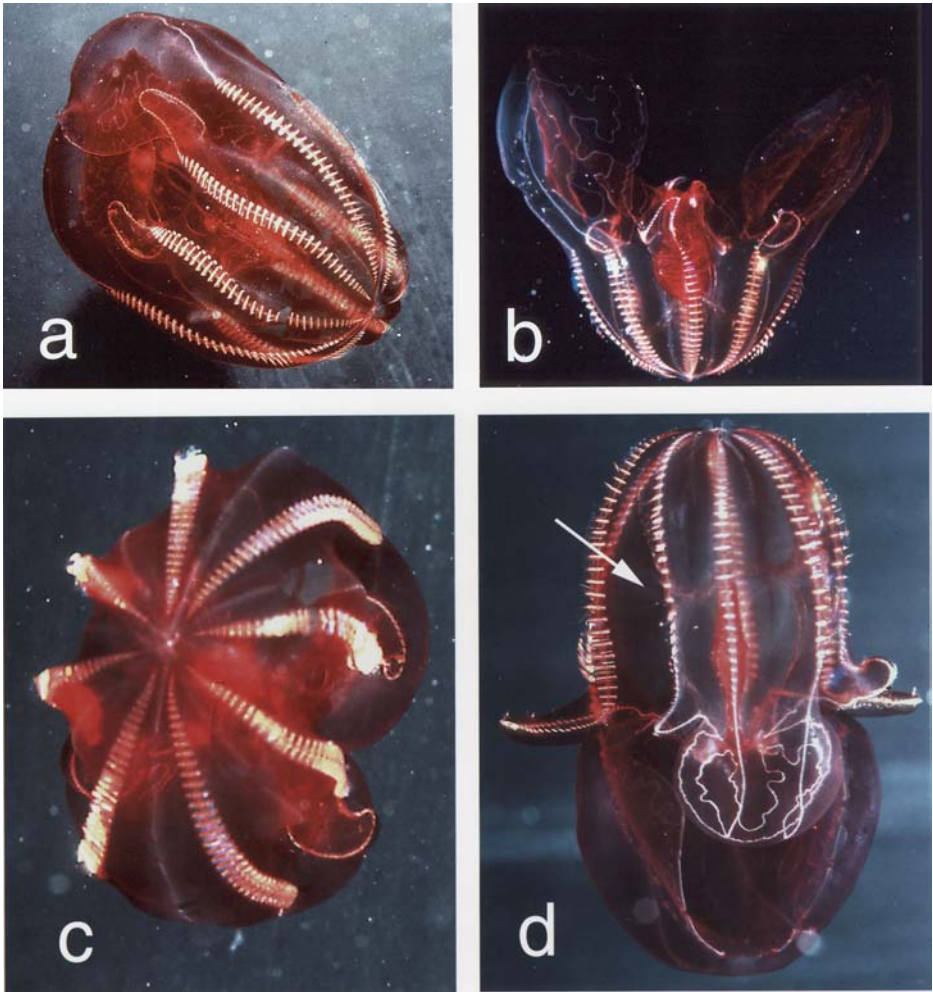


Figure 3. Four different specimens of *Lampocteis cruentiventer* collected in Monterey Bay and photographed in the laboratory. Scale lines for all figures = 1 cm. The position of the notch is indicated with an arrow. (a) Oblique view in the stomodaecal plane showing the extent of the notch. (b) View in the stomodaecal plane showing the canals in the oral lobes and one of the tentacle bulbs. (c) Aboral view showing the ridges and pole plates. This specimen is damaged—a large tear is visible in the upper right quadrant. (d) Oblique view in the tentacular plane. This specimen is regenerating one of the oral lobes; note that the canal pattern on the smaller oral lobe is much simpler than in the larger lobes of the same specimen and of the other specimens. The outline of the large notches and the pole plates can be seen.

approximately the level of the infundibulum. All meridional canals end blindly at their aboral ends. Auricles fleshy, relatively short and wide, with well differentiated comb plates. Tentacle bulbs large. Well-developed infundibular canal present, about one-third length of stomodaeum. Pole plates narrow and pointed. Oral lobes of moderate size, arising about two-fifths distance between mouth and aboral end of stomodaeum.

Description.—BODY, AURICLES, AND ORAL LOBES.—The body is slightly compressed in the tentacular axis, with the stomodaecal axis about 1.6 times longer than the tentacular axis at the level of the tentacle bulbs. Overall length (tip of oral lobes to aboral pole) of

holotype about 5 cm. MBARI specimens ranged between 1.5 and 16 cm in overall length and between 1.2 and 10 cm in width (measured in the stomodaeal plane). The 1.5-cm MBARI specimen was a fully developed lobate ctenophore, with no evidence of cydippid larval morphology.

The body is raised into 16 slight ridges, when viewed from the aboral pole. The comb plates sit on eight of these ridges, and the other eight ridges lie between the comb rows. These latter ridges are least pronounced between adjacent subtentacular comb rows, and most pronounced between adjacent substomodaeal comb rows. In addition, the body is excavated between adjacent subtentacular comb rows at the level of the infundibulum, forming a deep notch (Figs. 1A,2A,C,3D). This notch is difficult to see in the photographs, and is indicated with arrows. It is, however, very easy to see when living specimens are examined.

The consistency of the body is extremely firm, and the animal is not completely transparent, so that the internal connections of the gastrovascular system are sometimes difficult to determine. While the body of the holotype was tinted a light red, the color of the body in MBARI specimens ranged from almost transparent to a deep black-purple, with amber and red being the most common tints. The auricles are relatively short and wide, and are extremely fleshy. They appear incapable of much motility. The oral lobes of the holotype were also extremely fleshy and strong, but in larger specimens were much more delicate. The oral lobes are only a little longer than the body (measured from the mouth to the statocyst). In one MBARI specimen, one of the oral lobes was clearly being regenerated (Fig. 3D).

COMB ROWS.—The comb rows lie on eight of the body ridges. The substomodaeal comb rows and the adjacent body ridges are at approximately the same heights, while the subtentacular comb rows lie on higher ridges than the body ridges between them. The substomodaeal comb rows are slightly longer than the subtentacular comb rows. The substomodaeal comb rows end slightly below the auricles, whereas the subtentacular comb rows end slightly above them (Fig. 1A,B). In the holotype, the subtentacular comb rows had about 20 comb plates, while there were about 23 comb plates in the substomodaeal comb rows. In MBARI collections, the largest specimen had 42 substomodaeal comb plates and 39 subtentacular comb plates. The comb plates are extremely broad and prominent, thus creating a pronounced iridescence, which was so bright that it obscured the details of internal structure in some of the photographs. While the comb rows of most ctenophores have this property, it is more strongly developed in this species than in most others. The comb plates of the auricles (ca 43 in the holotype) are much smaller than the comb plates on the body.

STATOCYST AND POLE PLATES.—The morphology and location of the statocyst is similar to that in other ctenophores (Fig. 2C), and is slightly overtopped by the low body ridges. The pole plates are relatively long, and extended orally to about the level of the sixth substomodaeal comb plate in the holotype. In MBARI specimens, the pole plates extended to the sixth substomodaeal comb plate in smaller specimens and to the tenth substomodaeal comb plate in the largest. The pole plates are very slender and pointed, and lie on the crests of the ridges between adjacent substomodaeal comb rows.

TENTACULAR APPARATUS.—The tentacle bulbs lie close to the mouth opening, and are supplied by the tentacular canals (Fig. 1A,B). The tentacle bulbs are white, relatively large and prominent, and a mass of secondary tentacle filaments were sometimes be seen (Fig. 2B) extending from them and along the margins of the mouth opening (the oral

groove). In MBARI specimens, the tentilla were never seen extending onto the oral lobes, but were observed (in the laboratory) floating freely from the tentacle bulbs.

GASTROVASCULAR SYSTEM.—The mouth is located below the origin of the auricles and leads into a massive, blood-red stomodaeum (Fig. 1A,B). The mouth opening appears relatively narrow when viewed in the tentacular plane, but is widely flared into an oral groove when viewed in the stomodaeal plane, and its red lips are bordered with tentilla from the tentacle bulb. The stomodaeum appears diamond-shaped when viewed in the tentacular plane (Figs. 1A,2D), and flask-shaped when viewed in the stomodaeal plane (Figs. 1B,2B). In most other species of ctenophores, the stomodaeum appears flat when viewed in the tentacular plane, and is not capable of this type of expansion. None of the MBARI specimens showed the degree of expansion of the stomodaeum in the tentacular plane that was observed in the holotype: at most only a slight dilation was observed (Fig. 3D). The infundibulum is also massive, as are the gastrovascular canals that extend from it (Fig. 1). The infundibular canal is less than half the length of the stomodaeum, and opens aborally via two anal papillae. The paragastric canals are enormous and lie on the crests of gelatinous ridges extending along the margins of the stomodaeum. The diverticula of the paragastric canals are prominent, and can be seen even when the animal is viewed in the tentacular plane (Figs. 1A,2D). The paragastric canals flare out near the tentacle bulbs, but do not appear to connect with the tentacular canals. We could not determine whether or not the paragastric canals of the holotype had connections with the subtentacular meridional canals at the oral margins of the auricles, as is the case in many other lobate ctenophores. These connections were observed in MBARI specimens.

Four interrarial canals extend from the infundibulum. Each interrarial canal then branches to form two adradial canals (a subtentacular and a substomodaeal adradial canal). The subtentacular adradial canals are somewhat shorter than the substomodaeal adradial canals. All adradial canals enter the meridional canals at the level of the infundibulum. Tentacular canals arise from the infundibulum at the junction of the interrarial canals, travel beneath the surface of the notch toward the mouth, and supply the tentacle bulbs located on either side of the oral opening.

All of the meridional canals have blind aboral endings. The oral portions of the meridional canals connect with one another in the oral lobes as they do in most other lobate ctenophores. That is, the subtentacular meridional canals pass into the auricles, and then extend along the margins of the oral lobes, connecting with the other subtentacular meridional canal on the same oral lobe. Likewise, the substomodaeal meridional canals extend onto the oral lobes medially, wind complexly in the thick fleshy oral lobes, and finally unite with their counterparts on the same oral lobe.

GONADS.—The holotype did not appear to be sexually mature, since no traces of gonads were observed lying along any of the meridional canals. Gonads were not observed on any MBARI specimens.

VERTICAL DISTRIBUTION AND BEHAVIOR.—No observations on vertical distribution and behavior were recorded on the dive during which the holotype was collected, but the ROV VENTANA has observed more than 100 specimens in Monterey Bay. These specimens occurred between depths of 300 and 1012 m. Temperatures at which they were observed ranged between 4 and 9.5°C and the salinity was between 33.69 and 34.45‰. They were found over a wide range of oxygen concentrations (0.13 to 1.07 ml L⁻¹), and did not seem to avoid the region's prominent oxygen minimum layer. *L. cruentiventer* did not form aggregations in Monterey Bay, and the maximum number seen on a single 6-h dive was

four. Thus, this ctenophore seems to be a minor component of the Monterey Submarine Canyon pelagic community.

When observed in the field, *L. cruentiventer* usually swam diagonally upward in an oral direction, with their oral lobes expanded. They reacted to the turbulence created by the ROV by closing their oral lobes and swimming with the comb rows. They were never observed to swim by flapping their oral lobes. None were observed with food in their stomachs. No parasitic or commensal organisms were found on them, and no organisms were seen feeding on them.

DISCUSSION

OTHER REPORTS OF *LAMPOCTEIS CRUENTIVENTER*.—*L. cruentiventer* was originally called "*Lampoctena sanguineventer*" in an unpublished draft of this manuscript written by GRH. Unfortunately, this manuscript became widely distributed, so that the latter name was used by a number of deep-sea biologists. Vinogradov and Chindonova (1994) published a version of this name, referring to a deep-sea specimen that they observed as "the ctenophore *Lampactena*". A photo of a specimen of *L. cruentiventer* from Monterey Bay was published by Nybakken (1993, plate 25) and labeled "*Lampoctena sanguineventer*". This name was also included in an exhibit at the Monterey Bay Aquarium (Connor, 1991). The name "*Lampoctena sanguineventer*" can also be found on the World Wide Web.

Since no description has been previously published, the designation, "*Lampoctena sanguineventer*" is a nomen nudum, and we have chosen to use *Lampocteis cruentiventer* to avoid possible confusion. If the specimens reported by Vinogradov and Chindonova (1994) indeed belong to the same species as the one described in this paper, they found them distributed at much greater depths (2400 to 4600 m) than we did. However, we are skeptical of their identifications, as they were made without the collection and close examination of specimens, and there are other species of red-gutted lobate ctenophores in the deep sea (pers. observ.). A specimen resembling *L. cruentiventer* was observed in deep Atlantic water off St. Croix (L. P. Madin, pers. comm.), and a specimen that resembles ours was reported from Sagami Bay (Toyokawa et al., 1998, *Lobata* sp. A, fig. 3I). We cannot identify the latter specimen with certainty. Thus, while we expect that *L. cruentiventer* has a wide distribution in the deep sea, the only certain identifications at present are from the California coast.

DIFFERENCES FROM OTHER SPECIES.—*L. cruentiventer* can be distinguished from all other lobate ctenophores in three ways: (1) its remarkable stomodaeum surmounted by capacious paragastric canals with diverticula, (2) the unusual notches that almost create a hole through the animal, and (3) the blindly ending meridional canals. Several ctenophores with pigmented stomodaea have been described: *Bathocyctena chuni* (Moser, 1909); *Beroe abyssicola* Mortensen, 1927; *Bathocyroe paragaster* (Ralph and Kaberry, 1950); and *Bathocyroe fosteri* Madin and Harbison, 1978.

B. abyssicola can be immediately excluded since it has no tentacles, and has all of the morphological features of other members of the order Beroida (among those features that distinguish it from *L. cruentiventer* are a lack of oral lobes or auricles, a short infundibular canal, and no interradiial canals). Further, the molecular sequence of *L. cruentiventer* obtained thus far is distinct from the sequences obtained for species of *Beroe* and *Bathocyroe* (as well as other lobate ctenophores) (Matsumoto, unpubl. results).

L. cruentiventer can be distinguished from both species of *Bathocyroe* in a number of ways. Both species of *Bathocyroe* have slender paragastric canals without diverticula, which extend to the margins of the oral lobes. The stomodaea of both species of *Bathocyroe* are small and compressed in the tentacular axis, and the auricles are very broad and flat. The oral lobes arise at about the level of the mouth opening, and they are much larger than the oral lobes of *L. cruentiventer*. All of the adradial canals connect to the aboral ends of the meridional canals.

Ralph and Kaberry (1950) also described and figured a cydippid ctenophore with a red stomodaeum, measuring 6 mm (with 20 subtentacular comb plates), which they considered to be the larva of *B. paragaster*. If this is the case, which we consider unlikely, then the development of *B. paragaster* is very different from other lobate ctenophores, since in their figure (Ralph and Kaberry, 1950, text fig. III), all of the adradial canals enter the meridional canals at about the level of the infundibulum, and thus all of the meridional canals end blindly aborally. In other cydippid larvae, the connection of adradial canals to the meridional canals resembles the adult condition at a very early stage. For example a 5-mm long *Mnemiopsis leidyi* Agassiz, 1865 larva with eight subtentacular comb plates clearly has all of the adradial canals entering the meridional canals at their aboral ends, just as in the adult (Mayer, 1912). Examination of field-collected juvenile *Eurhamphaea vexilligera*, which can be distinguished by their red ink sacs, shows that the adradial canals of very young larvae (5-mm long, six subtentacular comb plates) connect with meridional canals in the same manner as is seen in the adult (Harbison, pers. observ.). Moreover, their drawings of adult *B. paragaster* (Ralph and Kaberry, 1950, text fig. II) indicate that the adult, which measures 25 mm from the statocyst to the tip of the oral lobes, has fewer (17) subtentacular comb plates than their supposed larva. If this is not an adult cydippid, it could well be a larva of some deep-sea lobate closely related to *L. cruentiventer*. Besides the configuration of the adradial canals, the stomodaeum is very large, and the paragastric canal is extremely prominent, both features which are characteristic of the adult *L. cruentiventer*, rather than the adult *B. paragaster*. However, it cannot be a larva of *L. cruentiventer*, since our holotype, which is much larger than the cydippid, has only about 20 comb plates.

B. chuni could be a larval stage of *L. cruentiventer*, since it also has a red stomodaeum and paragastric canals with diverticula. However, its morphology strongly suggests that it is an adult cydippid. The tentacle bulbs are located deep inside the body near the infundibulum, and the tentacles exit close to the mouth through long sheaths. The size of the largest specimen, 30 mm, is much greater than that of the smallest MBARI specimens (15 mm), which already have auricles and oral lobes. Since all lobate ctenophore larvae that have been thus far described have tentacle bulbs that lie close to the surface of the body with short or non-existent tentacle sheaths, it seems very unlikely that *B. chuni* is a larval lobate.

RELATIONSHIPS OF *LAMPOCTEIS CRUENTIVENTER* WITH OTHER SPECIES.—Harbison and Madin (1982) recognized six families in the Lobata, five of which were monogeneric (Leucotheidae Krumbach, 1925, Eurhamphaeidae Agassiz, 1860, Bathocyroidae Madin and Harbison, 1978, Ocyropsidae Krumbach, 1925, and Kiyohimeidae Komai and Tokioka, 1940. Based on the morphology of *L. cruentiventer*, we suggest that the genera *Deiopea* (which Harbison and Madin, 1982, placed in the Bolinopsidae) and *Kiyohimea* be moved into the Eurhamphaeidae, to share it with *Eurhamphaea vexilligera*. The revised diagnosis for this family is: lobate ctenophores with extremely transparent bodies markedly

compressed in the tentacular plane. Oral lobes and auricles originating near the level of the mouth. Auricles short or of moderate size, rigid. Subtentacular adradial canals connecting with the meridional canals at about the level of the infundibulum (thus subtentacular meridional canals ending blindly aborally) and substomodaeal adradial canals connecting with the aboral ends of the meridional canals. Subtentacular meridional canals extending into aboral projections (*Eurhamphaea* and *Kiyohimea*) or body with no aboral projections present (*Deiopea*). Subtentacular comb rows longer than (*Eurhamphaea*) or approximately equal to (*Kiyohimea* and *Deiopea*) substomodaeal comb rows. Tentacular apparatus well developed (*Eurhamphaea*, *Deiopea*, and *Kiyohimea usagi* Matsumoto and Robison, 1992)) or greatly reduced (*Kiyohimea aurita* Komai and Tokioka, 1940).

The adradial canals of members of the genus *Leucothea* connect with the meridional canals in a similar way to those of members of the redefined family Eurhamphaeidae. However, the auricles are long and sinuous, and originate (as do the oral lobes) at about one-third the distance between the mouth and the statocyst. In addition, the substomodaeal, rather than the subtentacular portions of the body are raised into aboral projections. At this stage in our knowledge of the morphology of lobate ctenophores, we provisionally retain the monogeneric family, Leucotheidae.

The family Bolinopsidae contains only two genera, *Bolinopsis* and *Mnemiopsis*. The revised diagnosis of this family is: lobate ctenophores slightly compressed in the tentacular plane. Oral lobes and auricles originating at the level of the statocyst (*Mnemiopsis*) or about halfway between statocyst and mouth (*Bolinopsis*). All adradial canals connect with meridional canals at their aboral ends. Substomodaeal comb rows much longer than subtentacular comb rows. Tentacular apparatus well developed.

The genus *Ocyropsis* Mayer has morphological affinities with the Bolinopsidae. All adradial canals connect with the meridional canals at their aboral ends. However, they are extremely flattened in the tentacular plane, and the tentacular apparatus is greatly reduced (*Ocyropsis maculata*) or entirely absent (*Ocyropsis crystallina*). Therefore, just as we did with *Leucothea*, we provisionally leave this genus in its own family, the Ocyropsidae.

Likewise, the genus *Bathocyroe* has affinities with the Bolinopsidae and Ocyropsidae. All adradial canals connect with the meridional canals at their aboral ends. However, the paragastric canals pass into the oral lobes and are bordered with tentilla, the stomodaeum is very short, and the infundibulum is elongate, so that the origins of the interradi al canals lie aboral to the origins of the tentacular and paragastric canals. As with species of *Ocyropsis* (Harbison and Miller, 1986), *B. fosteri* swims by flapping the oral lobes and is dioecious (Miller et al., 2000). In spite of these similarities, we think it advisable to retain the family Bathocyroidae.

As more deep-sea lobate ctenophores are described, the relationships within the order will become clearer. We hope that our revised family diagnoses will provide a framework for a better understanding of evolution within the group. We stress that these diagnoses should be regarded as provisional, since our understanding of evolution within the Lobata is at an early stage.

ACKNOWLEDGMENTS

The authors would like to thank the pilots of the vehicles (ALVIN and VENTANA) for their expertise. E. Chase drew Figure 1, N. Swanberg took the photographs of the holotype (Fig. 2), and K. Raskoff photographed the animal in Figure 3B. This research was supported by grants to GRH (National

Science Foundation Grants OCE 77-22511 and DEB 78-23912) and to BHR and GIM (Monterey Bay Aquarium Research Institute).

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DATE SUBMITTED: January 18, 2000.

DATE ACCEPTED: December 21, 2000.

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